

An Early Cretaceous (late Albian) halecomorph (? Ionoscopiformes) fish from the Toolebuc Formation, Eromanga Basin, Queensland

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ABSTRACT

The partial neurocranium of a relatively small, halecomorph fish is described as *Canaryichthys rozefeldsi* gen. et sp. nov. and represents the first possible ionoscopiform from the Cretaceous of Australia. The specimen was collected from the marine Toolebuc Formation of the Eromanga Basin, near Boulia, in the central west of Queensland, deposited during the Early Cretaceous (late Albian) when an epeiric sea covered much of the centre of the State. It is undistorted and preserved in 3-dimensions but lacks all but the cranial vault. *Canaryichthys* has many features in common with the enigmatic English Jurassic 'caturid' neurocranium redescribed and figured by Patterson (1975) as '*Aspidorhynchus*' sp., (originally described by Rayner, 1948) and also appears to have affinity with the Early Cretaceous (Aptian), *Oshunia*, from South America. □ *Halecomorphi*, *Ionoscopiformes*, *Canaryichthys rozefeldsi*, '*Aspidorhynchus*', *Oshunia*, *Macrepistius*, *Early Cretaceous (late Albian)*, *Toolebuc Formation*, *Eromanga Basin*.

The partial neurocranium of the relatively small halecomorph fish described here as a new genus and species, was collected from near Boulia in central western Queensland, exposed from a coquinite of the Toolebuc Formation. This sediment was deposited as shallow-water, marginal, marine deposits of Early Cretaceous (Late Albian) age, in the western part of the Eromanga Basin, within the Great Artesian Superbasin (Jell, Draper & McKellar 2013). This area and these deposits have been known to contain numerous remains of marine reptiles, especially ichthyosaurs but the fossil fauna also includes plesiosaurs, pliosaurs and turtles, as well as rare pterosaurs and birds, with the latter considered to add support for the suggestion of an in-shore depositional environment. Fossilised remains of fish, especially sharks

and teleosts are also commonly encountered. Bartholomai (2004) has recorded the presence of the aspidorhynchid, *Richmondichthys sweeti* (Etheridge Jnr. & Smith Woodward 1891). The pachyrhizodid, *Pachyrhizodus marathonsensis* (Etheridge Jnr. 1905) has also been shown to be present (Bartholomai 1969, 2012). The Toolebuc pachycormid, *Australopachycormus hurleyi* Kear, 2007, was described from the Boulia area, while Kear & Hamilton-Bruce (2011) also record the presence of the ichthyodectiform, *Cooyoo australis* Lees & Bartholomai, 1986 from that area.

Cook (2012) regards the age of the Toolebuc Formation as being Early Cretaceous (Late Albian) but earlier work by Henderson (2004) has suggested the age be regarded as early Late Albian, based on ammonite and nannofossil

biostratigraphy. Smaller individuals and representatives of small species of fishes are infrequently encountered in the Toolebuc Formation and, when found in near shore deposits, are usually in a highly disassociated or fragmented state. It is considered unlikely that collections of better preserved and identifiable material relating to representatives of small taxa and immature individuals of larger species will be expanded in the near future.

The fossil record of the Halecomorphi is highly diverse (Brito & Alvarado-Ortega, 2013). However, most of the recorded Cretaceous occurrences have been from Northern and Central American deposits. Revisions and discoveries of the group over recent decades have concentrated on non-Gondwanan taxa and the presence of a broader halecomorph record in the Australian Cretaceous should lead to improved global understanding of the phylogeny of the group.

The holotype neurocranium that forms the basis for the description of the new taxon, *Canaryichthys rozefeldsi*, is preserved in an undistorted, 3-dimensional state, relatively common in many of the large individuals within fossil actinopterygian fishes from the Toolebuc Formation in the Boulia area and elsewhere in the marine Eromanga Basin sediments. Unfortunately, the holotype specimen lacks those characters considered by others to be phylogenetically diagnostic for determining halecomorph phylogenetic relationships. However, formal description of *Canaryichthys*, based on general comparisons with neurocrania of described halecomorphs, is felt reasonable, expanding the identified fish fauna of the Eromanga Basin and increasing knowledge of their Gondwanan radiation.

Abbreviations. acv = anterior cerebral vein fenestra; Apto = autopterotic; Asph = Autosphenotic; Boc = Basioccipital; Bsp = Basisphenoid; df = dilator fossa; Dpto = Dermopterotic; dlpto = descending lamina of dermopterotic; Epo = Epiotic; Exo = Exoccipital; fhm = hyomandibular facet; fica = foramen of internal carotid artery; fm = foramen magnum; foca = foramen for occipital artery; fpt = facet for ligament to post-temporal; Fr = Frontal;

frla = foramen of recurrent branch of facial nerve; fvoc = posterior cerebral vein fenestra; Ic = Intercalar; jc = jugular canal; Le = Lateral Ethmoid; Leas = Lateral Ethmoid attachment surface; Ors = Orbitosphenoid; osc = otic sensory canal; Pa = Parietal; Pro = Prootic; prlm = process for origin of branchial levator muscles; Pspa = Parasphenoid attachment area; Opo = Opisthotic; potb = prootic bridge; Pas = Parasphenoid; ptf = post-temporal fossa; Pro = Prootic; Pto = Pterotic; Pts = Pterosphenoid; So = supraorbital; sosc = supraorbital sensory canal; Sot = Supraotic; stf = subtemporal fossa; Soc = Supraoccipital; vfon = vestibular fontanelle; I = olfactory tract fenestra; II = optic fenestra; III = oculomotor nerve foramen; IV = trochlea nerve foramen; V = trigeminal nerve foramen; VI = abducens nerve foramen; VII = facial nerve foramen, IX = glossopharyngeal nerve foramen; X = vagus nerve foramen.

Neopterygii Regan, 1923

Holostei *sensu* Grande, 2010

Subdivision Halecomorphi, Cope, 1872

Order ?Ionoscopiformes Grande & Bemis, 1998

Family *incertae sedis*

Canaryichthys gen. nov.

Generic Diagnosis. As for the specific diagnosis until such time as additional species are recognised.

Etymology. Named for 'Canary' Station, near Boulia, Central West Queensland (CWQ), from which the type species was recovered.

Type Species. *Canaryichthys rozefeldsi* sp. nov.

Canaryichthys rozefeldsi sp. nov.
(Figs 1-3)

Holotype. QMF17025, partial neurocranium comprising the only the only known specimen at this time, from 'Canary' Station, SE of Boulia, CWQ, minimally prepared by mechanical techniques.

Etymology. Named for Dr Andrew Rozefelds (now Head of Geosciences, Queensland Museum), who collected and prepared the holotype specimen during his previous appointment in the geological section of the Queensland Museum.

Formation and Age. From the Toolebuc Formation of Early Cretaceous (Late Albian) age.

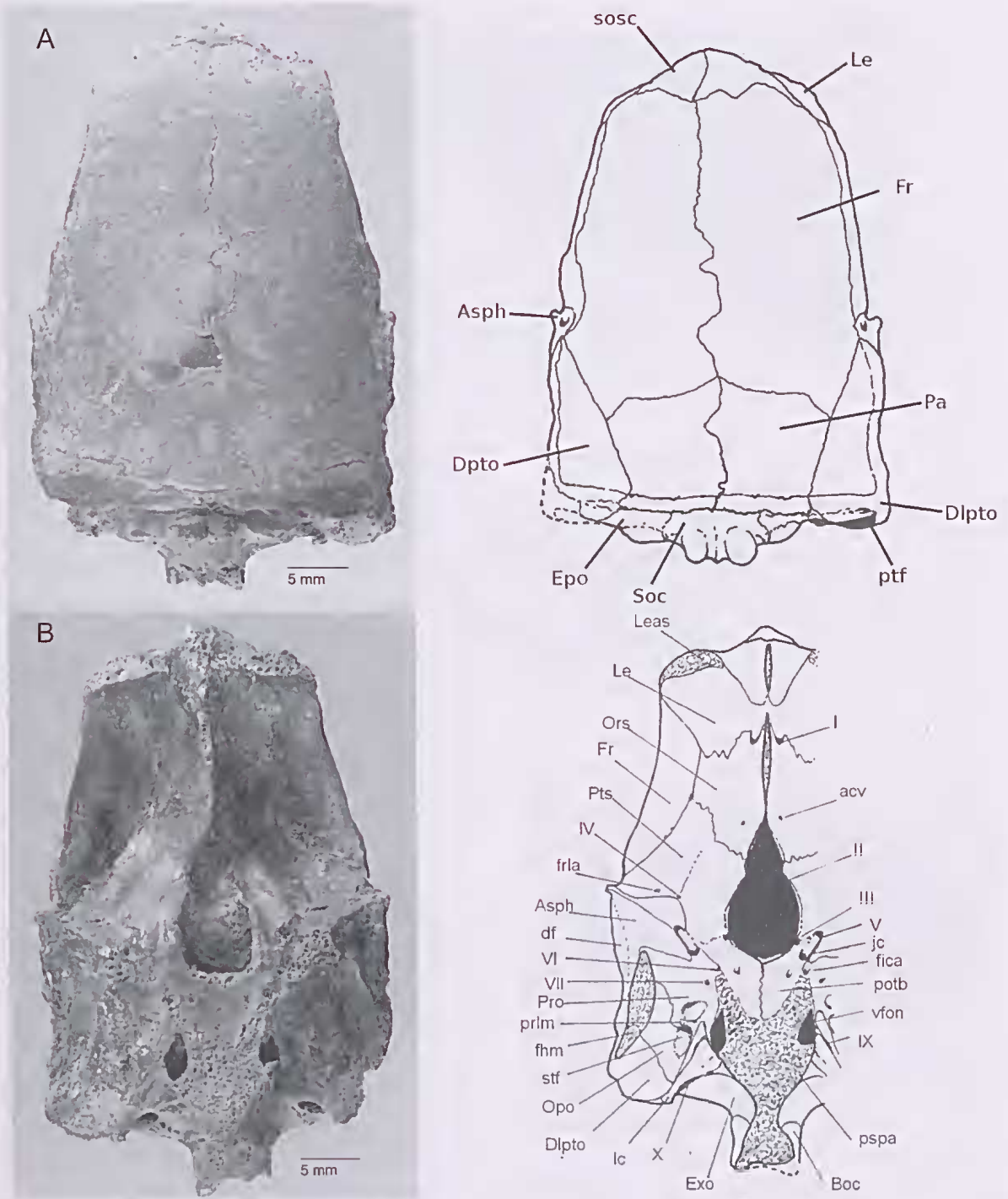


FIG. 1. *Canaryichthys rozefeldsi* gen. et sp. nov., QMF17025, Holotype. A, photograph and interpretive drawing of partial neurocranium in dorsal view. B, photograph and interpretive drawing of partial neurocranium in ventral view.

Specific Diagnosis. A small species with a shallow, broadly arched neurocranium, with sloping posterior surface. Skull roof ganoine covered with very fine 'orange skin' ornamentation internally with fine tubules often leading to minute surface pores. Frontals anteriorly stepped down and with interfrontal suture deeply interdigitating, especially posterior to orbits. Parietals with B:L ratio of 0.85, separated by deep, interdigitating suture. Cranial margins stepped down laterally and posteriorly. Circumorbital ring incomplete. Dermosphenotics only loosely attached to circumorbital margin, lacking inner orbital flange. Dermopterotics much longer than parietals. Post-temporal fossa angled anteromedially. Dilator fossa extends well onto autosphenotic. Short dorsal supraoccipital present, with prominent median bosses separating shallow, complex epiotics. Small pterotic present in post-temporal fossa. Exoccipitals very large, dished, meeting on broadly swollen, medial ridge above foramen magnum. Intercalar large, forming strong, grooved, elevated, ventrolateral bone fan. Nerve IX foramen in fold of intercalar fan. Vestibular fontanelle remnant present. No vertebral centrum fused with occipital condyle but basioccipital small, with very deeply, conically excavated notochordal pit. Vestibular fontanelle present. Subtemporal fossa small. Hyomandibular facet deeply concave, elongated, angled anteroventrally. Autosphenotic spine delicate. Pterosphenoid without pterosphenoid pedicle. Orbitosphenoid lacking ossified interorbital septum, firmly sutured to lateral ethmoid to form anterodorsal orbital margin. Parasphenoid reaching back of neurocranium and with process connected to base of autosphenotic.

Description. Neurocranium of this relatively small fish broad and shallow (see Figs. 1 and 2). Although lacking anterior, estimated length of skull is considered less than twice its maximum width (3 cm across both occipital and autosphenotic regions). Width across anterior of frontals 1.95 cm, while maximum depth of neurocranium at occiput is 1.89 cm. Cranial roof transversely relatively strongly convex (Fig. 2B) and slightly convex longitudinally. Anterior of neurocranium downturned at approximately 40°. Roofing bones ganoine covered and

extremely finely ornamented uniformly, with irregular short, low ridges separated by minute pits with ridges sometimes uniting into small rings around minute pockets (Fig. 1A). Stepped marginal areas not ornamented. Relatively numerous and elongated, slender tubules visible within ganoine, sometimes leading to surface pores, generally curving away from position of supraorbital sensory canal, especially medially and posteromedially from near centre of ossification of frontal.

Frontals comprise bulk of dorsal roof. Each meets its counterpart along a median suture deeply interdigitated behind orbits. Anterior of each frontal broad and stepped ventrally to accommodate overlap by the back of the anterior bones of skull roof, presumably including nasals. Lateral margin of frontal along and above orbital roof also stepped from autosphenotic to accommodate dermosphenotic (not preserved) but supraorbitals do not appear to have been present. Overall lateral margin of frontal part of the neurocranial roof slightly convergent anteriorly above orbit, while orbital margin very slightly concave laterally. Supraorbital sensory canal completely covered with no surface ridge. A small foramen present midway between median suture and lateral margin on anterior step believed to accommodate supraorbital sensory canal into frontal. Anteriorly, frontal partially overlies anterior of lateral ethmoid.

Parietal moderately large, longer than broad (B: L ratio of right parietal ca. 0.85), ornamented similar to frontals but with less obvious tubules visible in ganoine. Each does not reach as far anteriorly as front of dermopterotic. Median suture deeply and irregularly interdigitated. Posterodorsally, parietal widely separated on stepped margin by supraoccipital. Parietal meets epiotic along posterior neurocranial step with a very short contact with dermopterotic posterolaterally above inner margin of post-temporal fossa.

Dermosphenotic not preserved, not fused to frontal or dermopterotic along their very short junctions. From the stepped surface present on the frontal, the bone was probably small,

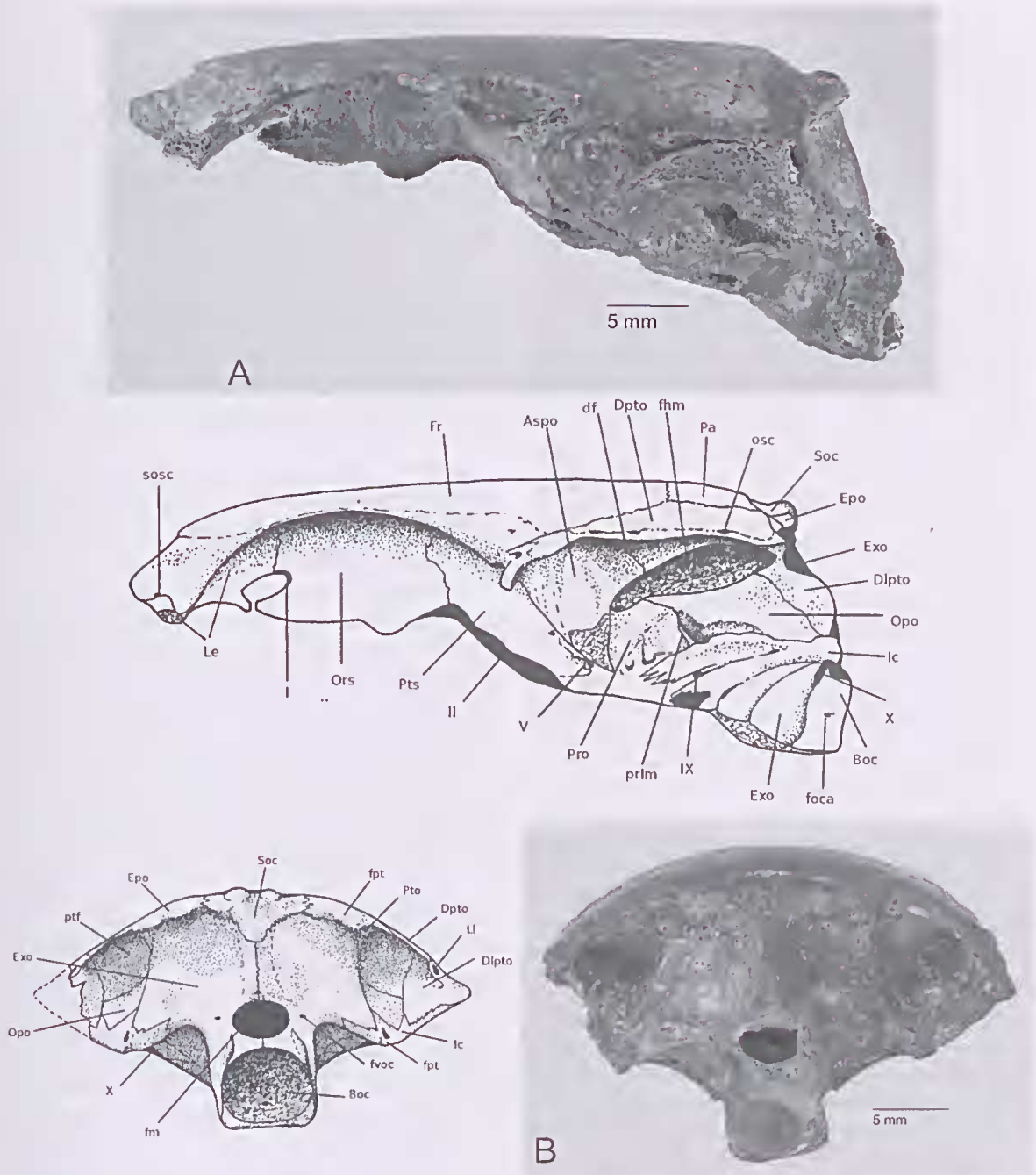


FIG. 2. *Canaryichthys rozefeldsi* gen. et sp. nov., QMF17025, Holotype. A, photograph of partial neurocranium in left lateral view above interpretative drawing. B, photograph of partial neurocranium in posterior view, beside interpretative drawing (slightly rotated anteroventrally to emphasise posterodorsal bones).

longer than broad and subovate in shape. A dorsal groove and indentation in rim of orbital wall present just in front of the autosphenotic spine, probably associated with sensory canal foramen directed ventrolaterally on the dorsal surface of the autosphenotic. No evidence of a ventral flange wrapping slightly around anterior of autosphenotic.

Dermopterotic with moderately large dorsal surface expression, ornamented similar to frontal. Lateral and posterodorsal margins bevelled and, except for minor contribution from autosphenotic, lateral edge provides roof for relatively deep dilatator fossa and bears otic sensory canal, with rare pores to surface, often within small processes above fossa roof. Canal opens posterolaterally above relatively large, external part of descending lamina of dermopterotic. Larger foramen opening posteriorly near dorsolateral margin of post-temporal fossa believed for entry of lateral line. Bone transversely and shallowly grooved just anterior to posterodorsal margin, with groove carrying numerous, minute pores. Descending lamina of dermopterotic provides posterolateral margin and wall of post-temporal fossa and appears to contribute to posterior of hyomandibular facet. Junction with opisthotic indistinct. Minor process of dermopterotic at dorsomedial rim of post-temporal fossa, lateral to epiotic adding support for supratemporal. Inside fossa, it extends anteriorly forming posterodorsal part of the inner wall, possibly uniting anteriorly with prootic. It appears to meet upper part of lateral margin of exoccipital along poorly defined junction near posterior of inner wall of post-temporal fossa.

Posterior neurocranial surface angled posteroventrally at angle of approximately 20° to vertical, with articulatory condyle for vertebral column projecting posteriorly even further (Fig. 2A). Sutural relationships of posterior neurocranial surface generally difficult to determine.

Supraoccipital relatively small, complex, extending broadly onto stepped, posterodorsal surface of neurocranium. Two prominent bosses present close to mid-line along posterodorsal neurocranial rim. Sutures with exoccipitals difficult to see at midline. Posterior surface

scooped dorsolaterally and continuing below epiotic (Fig. 2B).

Epiotic sturdy sutured medially to supraoccipital to provide epiotic process. Dorsally, epiotic meets parietal along base of posterior stepped margin and laterally has minimal contact with dermopterotic above the medial margin of the post-temporal fossa. Dorsomedially it carries a low swelling near junction with supraoccipital, apparently as support for supratemporal. Posterolateral surface ventrally scooped and broadly rounded onto medial wall of post-temporal fossa, meeting exoccipital ventrally. Posteromedially and within the dorsal margin and back of post-temporal fossa, it underlies dermopterotic. Epiotic process reduced.

Pterotic small, difficult to see, with anterior extent unknown, seen within post-temporal fossa as part of its inner wall, posteriorly meeting epiotic and dermopterotic dorsally.

Exoccipital forms largest element of posterior neurocranial surface. Junction with its counterpart present along base of foramen magnum; exoccipital provides lateral and dorsolateral margins of foramen magnum and extends dorsally to meet its counterpart along midline of broadly swollen, anterodorsally angled dorsoventral ridge from foramen magnum. Medial suture obscure. Element sharply flexed anteroventrally at level of top of foramen magnum and surface penetrated laterally by small foramen for posterior cerebral vein. Posterodorsal surface fanned and dished dorsolaterally, firmly fused with intercalar and epiotic. Below foramen magnum, it meets basioccipital just anterior to articulation for vertebral column; suture to basioccipital along the lateral neurocranial surface to near the posteroventral corner of intercalar, providing roof of foramen for nerve X.

Intercalar large, extending and expanding anteroventrally on lateral surface of neurocranium as longitudinally grooved, fan-shaped ridge of membranous bone from near lower corner of post-temporal fossa to cover most of anterolateral junctions between prootic and other elements and appears to meet flange from posterior process of parasphenoid. Intercalar provides posteroventral corner of subtemporal

fossa and supports narrow ridge dividing subtemporal fossa. Posteriorly, it surrounds lower margins of foramen for vagus nerve. Foramen for glossopharyngeal nerve contained in longitudinal flexure in anteroventral fan of intercalar, below subtemporal fossa. Sharply defined, anterodorsal ridge divides subtemporal fossa anteriorly, apparently above the prootic-opisthotic junction, probably providing an origin for branchial levator muscles.

Posterior of basioccipital preserved but anterior lacking. Articulating condyle includes very deep, conical notochordal pit, lined with dense, smooth, apparently lamellar bone. A small foramen, presumably for occipital artery, present laterally towards posteroventral rim of condyle. Anteriorly, large opening present above the element, representing remnants of vestibular fontanelle. Basioccipital contributes small dorsal process at ventrolateral margin of foramen magnum as vertebral condyle.

Opisthotic meets descending lamina of the dermopterotic to contribute significantly to the posterior of dorsolateral neurocranial surface. It meets prootic anteriorly and intercalar ventrally. Junction with prootic difficult to define but appears to be generally inclined anterodorsally before looping around front of deeply concave and anteroventrally angled, prominent hyomandibular facet. Subtemporal fossa is restricted but relatively deep above fan of intercalar

Prootic forms bulk of anteroventral lateral face of neurocranium. Dorsally, it meets dermopterotic at anterior edge of hyomandibular facet. Anteriorly, a small foramen present near side of roof of posterior myodome, interpreted as for internal carotid artery. Slightly above this is an indistinct foramen for nerve VII. Anterolaterally, a well-defined groove extends from foramen for nerve V back to foramen, possibly for entry of jugular canal. Medially directed plate of prootic meets its counterpart to form prootic bridge (Fig. 1B) above posterior myodome and is penetrated by a foramen, possibly for abducens nerve. Lateral to this is small foramen interpreted as for passage of facial nerve.

Autosphenotic relatively large, with a ventromedially angled sharp ridge to a delicate, well defined, anteroventrally projecting autosphenotic spine. Lateral face larger posterior to sharp ridge than the anterior. Foramen for recurrent branch of facial nerve present near margin of anterolateral face; several small foramina for ascending branches of superficial ophthalmic nerves also occur on anterior face. It meets prootic at anterior of hyomandibular facet, skirts anterodorsal margin of facet before turning anterodorsally then extended into short posteriorly narrowing process below dermopterotic margin of dilator fossa. Dorsal surface very small and is unornamented; surface penetrated above and posterior to autosphenotic spine by large foramen for anterior of sensory canal leading to shallow groove and marginal gap, below excavated shelf interpreted for dermosphenotic.

Pterosphenoid large, surrounding side of large opening for optic nerve. It smoothly and slightly bulges and, with anterior face of autosphenotic, forms the posterodorsal margin of orbit. Posteroventrally, it contributes to well-defined groove leading from foramen interpreted as being for trigeminal nerve, while foramen for oculomotor nerve exists at anteromedial edge of opening of optic nerve opening and outside scar for basisphenoid junction. No evidence exists for presence of pterosphenoid pedicle. Close to junction with autosphenotic, pterosphenoid penetrated by foramina for trochlear nerve and possibly that for recurrent branch of facial nerve. Anteriorly, bone firmly sutured to orbitosphenoid.

Orbitosphenoid relatively large, anteriorly surrounds central foramen for olfactory nerves. Ventromedially, bone lacks an ossified interorbital septum but is roughened, suggesting cartilagenous connection towards upper surface of parasphenoid. It also forms anteriorly 'V'-shaped anterodorsal roof of optic foramen. Small foramen for anterior cerebral vein present towards middle of bone.

Lateral ethmoid relatively short and firmly united with base of frontal, extending anteriorly from near middle of orbit to below stepped margin of the frontal. Broad plate of bone angled

anterolaterally beside anterolateral base of orbitosphenoid, thickening towards its roughened end. Anteriorly, its dorsal surface extends anterior to frontal and is slightly angled ventrally. Element linked to counterpart along a narrow, medial ridge that extends from its anterior extremity, posteriorly to short spine above foramen for olfactory nerves, approaching but not contacting an anteromedial spine of orbitosphenoid also above foramen for olfactory nerves. Body of bone curves anteroventrally, broadening from its junction with anterior margin of orbitosphenoid, with its end suggesting a cartilage junction to anteroventral neurocranial elements, most probably a pre-ethmoid. It has smoothly curved posteroventral surface forming anterodorsal margin of orbit.

DISCUSSION

Description of *Canaryichthys rozefeldsi* gen. et sp. nov., adds to the diversity of neopterygian halecomorph fishes in the marine, Early Cretaceous (Albian), Toolebuc Formation sediments of the Eromanga Basin. Known only from the western rim of the Basin, from near Boulia, CW Qld, the species co-existed in that area with *Richmondichthys sweeti* (Etheridge Jnr. & Woodward 1891), revised by Bartholomai (2004) and *Australopachycoruuus hurleyi*, described by Kear (2007), representatives of the halecomorph orders Aspidorhynchiformes and Pachycormiformes respectively. Remains of other, as yet undescribed marine halecomorphs are known from largely incomplete or fragmentary fossils from the Toolebuc and contemporaneous Allaru Formations in the collections of the Queensland Museum. Although the partial neurocranium of *Canaryichthys* is preserved in a three-dimensional, undistorted condition, it unfortunately presents none of the characters considered by other researchers to be unquestionably diagnostic for its reference to any of the recognised halecomorph orders. The general characters presented in the neurocranium show that the species cannot be assigned to either of the previously described Eromanga taxa. Older marine Cretaceous deposits of mainly Aptian/ Early Albian age in the Eromanga Basin are noted to have a broad

reptilian fauna but only rarely have fish remains been recorded (Cook *et al.* 2014). Similarly, even the earlier Jurassic Gondwana fish record, as reported by Lopez-Arbarello *et al.* (2008), is highly incomplete both stratigraphically and geographically. They observe that this limits the ability to suggest phylogenetic relationships taking account of earlier fishes of the Southern Hemisphere.

The current study thus draws on comparison of the neurocranium of *Canaryichthys* with those described halecostome genera having general skull morphology similar to the new species, such comparisons suggesting the species is probably referable to the Order Ionoscopiformes (see Fig. 3). Relevant neurocranial characters were also compared in published data matrix analyses in Grande & Bemis (1998) for *Ionoscopus cyprinoides* from the Late Jurassic, Solenhofen Limestone of Germany, for *Oshunia brevis* from the Early Cretaceous, Santana Formation from Brazil, for the European *Ophiopsis procera* and for *Macrepistius arenatus*, from the Early Cretaceous (Albian) of Texas.

Grande and Bemis (1998) provided a cladistic analysis of the Halecomorphi based on 69 morphological characters mainly focused on the Amiidae and their study included both Caturoidea and Ionoscopiformes, among others, as outgroups. They indicated that groups closer to the Amiidae received more complete taxonomic coverage than more distantly related groups, like the caturoids and ionoscopiforms. The Amiiformes, including the caturoids, are defined by three characters, only two of which relate to *Canaryichthys*. These are the presence of an opisthotic and the presence of a pterotic. Grande & Bemis (1998) however, contradicted this by noting that the pterotic is absent in caturids, sinamiids and amiids. Of the characters defining the Caturoidea, none are represented in the partial neurocranium of *Canaryichthys*. Three characters were determined to define the halecomorph Section B (unnamed by Grande & Bemis 1998) that included the Amiiformes and the Ionoscopiformes. Of these, only the condition of the dermosphenotic has relevance to comparison with *Canaryichthys*.

This character is stated to be usually firmly sutured into the skull roof in adult halecomorphs, but must have been only loosely attached in *Canaryichthys* because it is missing and represented by a possible scar on both sides of the skull. Of the two characters identified as diagnostic for the Ionoscopiformes, the first refers to an inner-orbital dermosphenotic flange, not present in *Canaryichthys*. The other relates to parietal shape, where the parietal width to length ratio of 0.85 falls below the upper limit of 0.90, determined by Grande & Bemis (1998) for the order. However, they note that this character is homoplasious and polymorphic in the ophiostids, *Ophiopsis* and *Macrepistius* and is therefore of no value in interpreting phylogenetic relationships in these groups. Subsequent cladistic analyses by Alvarado-Ortega & Espinosa-Arrubarrena (2008) on the early Cretaceous, ionoscopiforms *Quetzalichthys* and *Teoichthys*, from the Early Cretaceous (Albian) Tlayua Formation of Mexico, regard the parietal character as plesiomorphic. Analysis of *Cipactlichthys*, also from Mexico, by Brito & Alvarado-Ortega (2013) who referred it to the Ionoscopiformes, does not include any additional characters, than those previously identified in Grande & Bemis (1998), that are relevant to understanding the phylogenetic relationships of *Canaryichthys*. Similarly, the analysis in Lopez-Arbarella *et al.* (2014) for the Triassic (?Ladinian) ionoscopiform, *Archaeosemionotus* of Europe does not provide additional characters relevant to the placement of *Canaryichthys*. Modifications to the phylogenetic relationships in this group, however, were proposed, as new taxa were described and with the reassessment of existing forms such as *Furo*.

The dermopterotic in *Caturus furcatus*, (illustrated in Grande & Bemis, 1998) is generally very expanded posteriorly and significantly longer than the parietal; supraorbitals are present in *C. furcatus* but are mostly absent in ionoscopiforms depicted; the presence of an opisthotic in ionoscopiforms contrasts with the caturids where it is absent. A small pterotic is present in *Canaryichthys* but is absent in caturids; unlike most halecomorphs,

the dermosphenotic is interpreted to be only loosely attached to the skull roof and no inner orbital flange appears present; and a supraoccipital is present. Regarding the occiput and occipital condyle, Grande & Bemis (1998) observed that those halecomorphs lacking ossified centra, such as the caturids, had occiputs that are difficult to interpret, with basioccipital/exoccipital sutures sometimes missing. The occiput in *Canaryichthys* involves the basioccipital, with the exoccipital only contributing to the base of the condyles. Based on these insights qualified reference of *Canaryichthys* to the Ionoscopiformes, as defined by Grande & Bemis (1998), rather than to the Caturidae seems preferable. The phylogenetic relationship of *Canaryichthys* within the order is not clear.

Our understanding of halecomorph phylogeny largely builds on Grande & Bemis (1998) who noted that 'many of the non-amiid halecomorph groups needed comprehensive phylogenetic study, using modern preparation techniques and new material including Ionoscopiformes'. With the description of new fish, the record of halecostomes has improved significantly, in part, due to the new discoveries from Mexican and Brazilian early Cretaceous deposits. Cladistic analysis of the Ionoscopiformes by Alvarado-Ortega & Espinosa-Arrubarrena (2008) recognised two monophyletic families, the Ionoscopidae and the Ophiopsidae, adding the Early Cretaceous genera *Quetzalichthys* from Mexico and *Oshunia* from Brazil to the ionoscopids (the latter previously having been placed in a separate family, the Oshuniidae by Grande and Bemis, 1998). *Taoichthys* from the Early Cretaceous of Mexico was added to the Ophiopsidae by Alvarado-Ortega & Espinosa-Arrubarrena (2008), as well as *Macrepistius*, supported by an additional species of *Teoichthys* by Machado *et al.* (2013). Brito & Alvarado-Ortega (2013) added their Early Cretaceous Mexican taxon, *Cipactlichthys*, as a monophyletic sister group of the Ionoscopiformes + Amiiformes. The relationships within the ionoscopiforms were further addressed by Lopez-Arbarella *et al.* (2014), who concluded that *Furo*, *Archaeosemionotus* and *Robustichthys*

(see Xu *et al.* 2014) form a clade, and they included *Macrepistius* within the Ophiopsidae. Based on the Grande & Bemis (1998) analysis, summarised previously above, the familial relationships of *Canaryichthys* can only be regarded as *incertae sedis*. Incompleteness of the holotype of *Canaryichthys* precludes it contributing significantly to resolution of the arguments relating to relationships within basal neopterygians (see Gardiner *et al.* 1996) but it does add to a better understanding of the morphology of the bones often masked by dermal elements.

Comparison of the neurocrania of *Canaryichthys* and *Ionoscopus*, here illustrated in Figs. 3A and 3B, shows considerable broad similarities, supporting a possible relationship within the Ionoscopiformes. However, the cranial vault in *Ionoscopus* is incompletely ossified and the opisthotic is very small and only weakly in contact with surrounding bones (Massey, 1999). Like *Canaryichthys*, its pterotic is small, wedged between the dermopterotic and epiotic within the post-temporal fossa. It does, however, have a supraotic bone, lacking in *Canaryichthys*. The posterior neurocranial surface in both is similarly sloped and the cranial vault is shallow. The parasphenoid process extends over more of the autosphenotic in *Ionoscopus*.

Reasonable superficial similarity also exists between the preserved neurocranium of *Canaryichthys* and the partial crania described and illustrated by Rayner (1948) as '*Aspidorhynchus*' sp. from Middle Jurassic (Bathonian) sediments of Great Britain (Figs. 3B and 3C). It was subsequently regarded as a caturid by Patterson (1973), who suggested it was intermediate between the Jurassic *Heterolepidotus* and the Cretaceous *Macrepistius*. Patterson (1975) undertook a further revision and restoration of this neurocranial material referring to it again as an undescribed caturid, '*Aspidorhynchus*' sp. This material was later given attention by Gardiner *et al.* (1996), who suggested that the presence of a pterotic and opisthotic and the non-sutured condition of the dermosphenotic conflict with it being firmly referred to the Caturidae and it was regarded

as 'enigmatic'. '*Aspidorhynchus*' sp. was omitted from their phylogenetic analysis of the fossil halecomorphs because it was too incompletely known. The slightly inclined posterior intracranial surface in *Canaryichthys* differs from the near-vertical posterior in '*Aspidorhynchus*' sp. It also differs in lacking a supraotic, present posterodorsally in '*Aspidorhynchus*' sp. The cranial vault width to depth ratio of 1.80 in *Canaryichthys* is considerably larger than the 1.33 in '*Aspidorhynchus*' sp., the supraoccipital is present and the epiotic is much less developed. The Queensland taxon also possesses a prominent, deep, inclined hyomandibular fossa and has a much smaller prootic, a larger and inclined opisthotic and a larger autosphenotic. The foramen for nerve IX in *Canaryichthys* lies in a fold of the intercalar while that in '*Aspidorhynchus*' sp. enters directly onto the prootic. Maisey (1999) concluded that '*Aspidorhynchus*' sp. 'may belong to an ionoscopid or some closely related halecomorph'. Although *Canaryichthys* shares some similarities with '*Aspidorhynchus*' sp., they do not appear to be closely related.

Gardiner *et al.* (1996) noted that the braincase in '*Aspidorhynchus*' sp. is 'remarkably similar (both in general appearance and in many details) to the braincase of *Oshunia*,' originally regarded as an Ionoscopiform by Wenz & Kellner (1986) and revised and illustrated by Maisey (1991). *Oshunia* is from the Lower Cretaceous (Aptian) Santana Formation of the Araripe Basin of Brazil. It was photographically illustrated in Grande & Bemis (1998) and had additional morphological detail added by Maisey (1999). The drawing here presented in Fig. 3D is based on the photograph and drawings of a near-complete, acid-prepared specimen of *Oshunia* figured in Maisey (1999).

The lateral aspect of the neurocranium of *Canaryichthys* (Fig. 3B) shows it has somewhat more strongly inclined posterior neurocranial and orbital surfaces than *Oshunia* (Fig. 3D). A supraotic bone present in *Oshunia* is lacking in *Canaryichthys*. The parietals are relatively longer in *Canaryichthys* and their sutural contact with the frontals is much less interdigitated. Further, *Oshunia* does not have a pterotic bone, present in the Queensland taxon. The prootics

in both are relatively of similar size but, while the opisthotic is much smaller in *Oshunia*, it is firmly attached to the surrounding bones (Fig. 3D). The supraoccipital separates the epiotics in *Canaryichthys* and there are two rounded, posterodorsal bosses near the midline. The supraoccipital is not present in *Oshunia* where the epiotics (= epioccipitals in Maisey, 1999) have an extensive suture. The exoccipital in *Canaryichthys* does not extend anterior to the foramen for the vagus nerve and the autosphenotic is only slightly relatively larger. Loss of the base of the neurocranium in *Canaryichthys* has exposed a ventrolateral void that most probably represents the remaining area of the vestibular fontanelle. The process from the intercalar, like that in *Oshunia*, provides the origin for the branchial levator muscles and is very well defined near the middle of the small but relatively deep subtemporal fossa in *Canaryichthys*. In dorsal view, Maisey (1991) indicates that the frontals in *Oshunia* are constricted above the orbits, then widen again over the ethmoid region. Those in *Canaryichthys* (Fig. 1A) narrow slightly. The lateral aspect of the neurocranium in *Oshunia*, shows that apart from the presence of a strongly developed, posterior dermopterotic spine, *Oshunia* has almost as many general morphological similarities with *Canaryichthys* as does '*Aspidorhynchus*' sp. (Fig. 3C). Gardiner *et al.* (1996) provide a detailed comparison of the basal neopterygians, including *Oshunia* and *Macrepistius areuatus*, revised by Schaeffer (1960) and supported by further description of the neurocranium of the latter taxon in Schaeffer (1971). *Macrepistius* is regarded as an ophiopid by Alvarado-Ortega & Espinosa-Arrubarrena (2008) along with *Teoichthys* (differing from *Canaryichthys* by possession of a series of supraorbital bones). The anterior foramen for the supraorbital sensory canal in *Canaryichthys* is similarly positioned with regard to the possible nasal to that in *Caturus porteri*, described and figured by Rayner (1948), a character that is not, however, considered to provide insights into relationships. However, although close relationship of *Canaryichthys* with *Oshunia* is unlikely, its reference to the ionoscopids is possible, based on the overall,

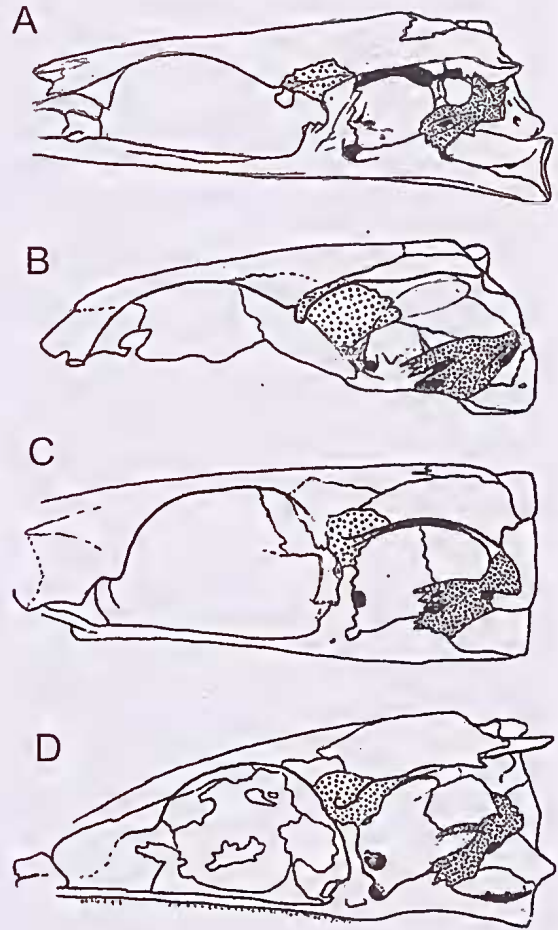


FIG. 3. Lateral view of neurocrania (not to scale) in the following- A, *Iouoscopus cyprinoides* (from photograph and drawing in Maisey, 1999); B, *Canaryichthys rozefeldsi* gen. et sp. nov.; C, '*Aspidorhynchus*' sp. (from Rayner, 1948); and D, *Oshunia brevis* (from photograph and drawing in Maisey, 1999). Dense stipple for intercalar and sparse stipple for autosphenotic.

broad similarities exhibited in its neurocranial remains.

Having regard to the comparisons with the genera discussed by Gardiner *et al.* (1996), the following notes are also considered to be relevant. Although the ascending process of the parasphenoid in *Canaryichthys* is not preserved, the scar left on the lateral surface of its braincase shows it most probably met

the lateral face of the autosphenotic towards its base, relatively lower than in *Oshunia* and '*Aspidorhynchus*' sp. Gardiner *et al.* (1996) regard the shortened parietals as primitive, although that in *Canaryichthys* with a W: L ratio of 0.85 is relatively close to the limit proposed for ionoscopiforms. The dermopterotic in the Queensland taxon is much longer than the parietal, unlike that in *Macrepistius* and more like that in other ionoscopids, as seen in *Oshunia*. The pterotic is also recorded as primitively present in extinct, non-amiid halecomorphs but is developed differently from one group to another. It is relatively small and present within the post-temporal fossa in *Canaryichthys* and in both *Oshunia* and *Ionoscopus*, as well as in '*Aspidorhynchus*' sp.

The intercalar in *Canaryichthys* (Fig. 2A) extends as a fan over the lower part of the saccular chamber that appears to have met the posterior process of the parasphenoid, as in *Macrepistius*, *Oshunia*, *Ionoscopus* and a number of other halecomorph fishes, a feature considered a possible synapomorphy by Gardiner *et al.* (1996). The orbitosphenoid is well developed in *Ionoscopus*, *Oshunia* and *Macrepistius*, similar to that in *Canaryichthys*. There is no evidence for the presence of an ossified interorbital septum in *Canaryichthys*, a well-developed structure in *Oshunia* and *Macrepistius* but the ventral base of the orbitosphenoid shows there was probably some cartilagenous interorbital septum development. The wide separation and spreading nature of the lateral ethmoids suggests that direct contact with the parasphenoid was unlikely in *Canaryichthys*. The bone probably contacted a pre-ethmoid, as in *Oshunia*, illustrated by Maisey (1991). *Canaryichthys* retains an opisthotic, as do non-amiid halecomorphs. The dermosphenotic was only loosely attached to the skull roof within a distinct, scarred recessed area within the autosphenotic and frontal. A shallow notch exists in the orbital margin in front of the autosphenotic spine but does not appear to have been associated with a flange that would have wrapped around the front of the spine. Until more complete material becomes available, further conjecture regarding the

phylogenetic significance of the element or its loss would be premature.

Ornamentation of the dorsal skull roof is similar to that in *Macrepistius*, as illustrated by Schaeffer (1971) but is much reduced in *Canaryichthys* (Fig. 1A). Bartram (1975) indicates the presence of ganoine tubules as ornamentation on dermal bones of the skull roof in the Upper Jurassic *Ophiopsis* from Europe (a genus also recorded from the Cretaceous of Brazil by Bartram, 1975 and Maisey, 1991). Tubules are visible within the ganoine in *Canaryichthys*. The dorsal aspect of the neurocranial roof in *Ophiopsis* has similar form to that in *Macrepistius* but is even more waisted above the orbits. The anterior shelf of the neurocranial roof in *Canaryichthys* descends at about the same angle from the rest of the roof as in *Macrepistius* but that in the former taxon is much shorter. Gardiner *et al.* (1996) recognised a monophyletic group that included *Oshunia* and *Ionoscopus*, as well as *Macrepistius*.

There appears to be slightly greater general morphological affinity present with the ionoscopid part of the group than with the ophiopsids. However, as noted above, diagnostic familial morphological characters are not preserved in the Eromanga specimen. Lopez-Arbarello, Rauhut & Moser (2008) indicated that ionoscopids were not represented in Gondwana faunas and were restricted to the Kimmeridgian-Tithonian of Europe, although the recent work by Alvarado-Ortega & Espinosa-Arrubarrena (2008) in describing *Quetzalichthys* from the Middle to Upper Albian limestones of Puebla, Mexico referred it to the Ionoscopidae and included *Oshunia* in that group, extended both stratigraphic and geographic limits for the family. *Quetzalichthys*, similar to *Oshunia*, had projecting processes from the posterior of the neurocranium. These were, however, more brush-like. As mentioned above, no such structure is present in *Canaryichthys*.

Brito & Yabumoto (2011) concluded that the southern and central American fishes had a close relationship with the Tethys fauna rather than supporting earlier ideas associating the fauna with the opening of the South Atlantic

Ocean. Regardless of the lack of firm ordinal and familial relationships between *Canaryichthys* and described ionoscopiforms, the taxon suggests a possible presence of greater ionoscopiformes radiation within the Gondwana fish fauna. Further discoveries from the Australian Lower Cretaceous sediments may shed additional information on Ionscopiformes relationships. The presence of *Canaryichthys* indicates the necessity for a broader overview of ionoscopiformes evolution generally.

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